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THE EFFECT OF PHOTOPERIOD ON THE REPRODUCTIVE DEVELOPMENT OF A PHOTOPERIOD SENSITIVE GROUNDNUT (*ARACHIS HYPOGAEA* L.) CV. NC AC 17090

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SUMMARY

The physiological basis for responses to daylength of a photoperiod sensitive groundnut genotype (NC Ac 17090) was investigated by comparing its growth and development in natural daylength with that in an artificially manipulated photoperiod in three field experiments. Photoperiod did not influence the thermal time to flowering, or the subsequent appearance of flowers until 900-950 flowers m^{-2} had appeared. Thereafter flowers continued to appear in short, but not in long, days. In each experiment, long days increased the thermal time between the initiation of each peg and pod, and the thermal time required for each fruit to mature. These fruit initiation and developmental changes were reflected in the partitioning of assimilates to pods, this being substantially less in long days than in short. Changes in pod initiation rate, partitioning co-efficient, and the thermal time taken for a pod to mature were related to mean daylength.

Marie-Luise Flohr, J. H. Williams y F. Lenz: *Efecto del fotoperíodo sobre el crecimiento reproductivo de un cacahuete* (Arachis hypogaea *L. - cv. NC Ac 17090) sensible al fotoperíodo.*

RESUMEN

Se realizaron tres ensayos de campos para estudiar la base fisiológica de las respuestas a la duración del día en un genotipo de cacahuete (NC Ac 17090) sensible al fotoperíodo, comparando su crecimiento y desarrollo bajo condiciones de duración diurna natural con el obtenido con un fotoperíodo manipulado por medios artificiales. El fotoperíodo no afectó el tiempo térmico hasta la floración ni la posterior aparición de flores hasta que llegaran éstas a las 900-950 flores m^{-2}. En adelante, las flores siguieron apareciendo en los días cortos pero no en los largos. En cada ensayo, los días largos aumentaron el tiempo térmico entre la iniciación de cada papila y vaina y el tiempo térmico necesario para que madurara cada fruta. Estos cambios en la iniciación y el desarrollo de la fruta se reflejaron en la repartición de los asimilados a las vainas, siendo en los días largos considerablemente menos que en los cortos. Los cambios en el ritmo de iniciación de la vaina, el coeficiente de repartición y el tiempo térmico que tardó en madurar la vaina estaban relacionados con la duración diurna media.

INTRODUCTION

Both temperature and photoperiod control the rate of progress to flowering in many grain legumes (Summerfield and Roberts, 1987; Roberts and Summerfield, 1987). However, in groundnut this aspect of development is little influenced by photoperiod (Fortanier, 1957). Since groundnut was considered to be day neutral, photoperiod has been neglected as a factor in the adaptation of this crop (Bunting and Elston, 1980). However, Wynne *et al.* (1973)

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showed that although photoperiod did not greatly influence the timing of flower initiation it did have a major effect on the pod yield of a number of groundnut genotypes. Emery *et al.* (1981) reported that this sensitivity of yield to photoperiod occurred after the start of flowering and Bell (1986), using data from a series of planting date trials, found a correlation between the mean photoperiod over the first 75 days and final yield.

Development of crops is strongly influenced by temperature between given cardinal values (Monteith, 1981); the base temperature for groundnut is about 10°C (Mohamed *et al.*, 1988).

Photoperiod sensitivity could be critical to the succesful transfer of improved groundnut genotypes to other daylength environments. Previous research has shown that photoperiod affects a wide range of genotypes differentially, changing yield-determining physiological parameters and quality characteristics (Witzenberger *et al.*, 1985). Crop growth rate is greater in long days, but the partitioning of this growth to the fruit, and/or the duration of rapid pod growth, are reduced in photoperiod-sensitive genotypes (Witzenberger *et al.*, 1988).

Previous research on groundnut has failed to define how photoperiod responses are affected and has only investigated differences in plant and crop responses at two extreme photoperiods, so that the nature of the response at intermediate daylengths remains unclear. This paper examines the influence of daylength on sequential steps in fruit initiation and yield determination across a range of (mean) photoperiods from 11.5 to 17.5 h, including a 4.0 h night break treatment.

MATERIALS AND METHODS

In a series of three experiments (two in the rainy season when the mean daylength was 13 h, and one in the post rainy season with 11.5 h days) the photoperiod sensitive genotype NC Ac 17090 was exposed to natural daylength (ND), and either a 4 h extension (LD) of the natural day (Experiments 1 and 2) or a 4 h illuminated night break (NB) between 2200 and 0200 h (Experiment 3). Illumination was supplied by 150 W incandescent tungsten filament lamps arranged in a grid over the field at a spacing of 3 × 3 m. All plants under the lamps were exposed to artificial light exceeding 60 lux at the canopy level. Illumination commenced at flowering and was continued until final harvest.

The experiments were sown at the ICRISAT Centre, (18° N, 78° E) in fields that had been fertilized with 60 kg ha^{-1} of P_2O_5 in the form of single super phosphate. The soil was an Alfisol with about 100 mm of available moisture in a 1.25 m profile. The land was prepared in a bed-and-furrow configuration with 1.5 m between furrows. Plant spacing in all experiments was 10 × 30 cm. Experiment 1, during the dry post-rainy season, received irrigations of 50 mm scheduled according to pan evaporation to meet the water requirements of the crop. Experiments 2 and 3 were rainfed (Table 1).

Table 1. *Meteorological data for the growth period of Experiments 1-3*

	Dec. 85	Jan. 86	Feb. 86	Mar. 86	April. 86	Total/Mean
Experiment 1						
Rain + irrigation (mm)	100	158	153	194	200	805
Evaporation (mm)	165	152	151	184	292	945
Solar radiation (MJ m^{-2} d^{-1})	17.5	15.8	16.2	19.1	22.3	18.2
	Jun. 86	Jul. 86	Aug. 86	Sep. 86	Oct. 86	Total/Mean
Experiment 2						
Rain (mm)	118	131	231	57	<1	538
Evaporation (mm)	262	221	146	173	190	991
Solar radiation (MJ m^{-2} d^{-1})	15.8	16.0	16.9	19.9	18.1	17.3
	Jun. 85	Jul. 85	Aug. 85	Sep. 85	Oct. 85	Total/Mean
Experiment 3						
Rain (mm)	89	173	46	76	93	477
Evaporation (mm)	230	183	168	160	152	893
Solar radiation (MJ m^{-2} d^{-1})	17.8	15.8	16.6	17.9	17.5	17.1

The numbers of freshly opened flowers were recorded on ten plants in each plot every morning. In Experiments 1 and 3 plant samples were taken at weekly intervals, and in Experiment 2 at fortnightly intervals. Sampling commenced after the photoperiod treatments were introduced. Plants were dug from a sample area of 0.8 m^2 in each of three replicates and all adhering soil washed off. Five plants were then selected at random from the bulk sample and their reproductive structures classified into aerial and subterranean pegs, and growing and mature pods. After being counted all these structures were dried in an oven at 80°C for 48 hours and then weighed. The growing and mature pods were shelled and their kernels counted and weighed. The area and dry weight of the leaves from a single plant were determined to estimate the specific leaf weight. The remaining plants were processed as a bulk sample, separated into leaf, stem and pod components, for which the dry weights were determined. Leaf area index (LAI) was estimated from the total leaf mass and the specific leaf weight.

In Experiment 1 the short-term distribution of assimilates was investigated by exposing plants to $^{14}CO_2$ for 10 minutes and measuring the distribution of the isotope 24 h later (Flohr, 1989).

The photoperiod (DL) of the LD and NB treatments was computed as

$$DL = 24 - D$$

where D is the mean of the longest continuous period of darkness within 24 hours. The hours of natural daylight were estimated as the average time between sunrise and sunset for the treatment period.

Because of the seasonal differences in temperature across the experiments, the passage of thermal time (TT) after sowing (TTAS) was computed by using maximum (Max) and minimum (Min) temperatures recorded at the metero-

logical observatory located within 500 m of all the experiments, using the equation below which assumes a base temperature of 10°C:

$$TT\ (°C\ d) = [(Max + Min)/2] - 10$$

The time taken for pods to mature was estimated as the TT (from fitted polynomial equations) between the time when 10% of the maximum pod number had been initiated, and when these pods had matured.

Pod growth rates (PGR) and crop growth rates (CGR) were estimated by linear regression over the phase of linear increase for these components, after adjusting for the higher energy content of pods relative to vegetative components as described by Duncan *et al.*, 1978. The partitioning coefficient (p) was estimated by dividing the energy-adjusted PGR by the energy-adjusted CGR.

RESULTS

Since the phenological responses to LD were similar in all experiments, only the data for Experiment 1 are used (as an example) to describe the effects of photoperiod on development. However, the PGR, CGR, reproductive development rates and other derived parameters for all three experiments are presented in the tables, since they were all used to evaluate growth and phenology responses to the five different photoperiods.

Total dry matter (TDM) and crop growth rates (CGR) were very similar in Experiments 1 and 2, but about 25% lower in Experiment 3. The effects of daylength treatments on the rate of biomass accumulation (Fig. 1a) were not significant and the trends between experiments were inconsistent (Table 2).

Table 2. *Crop growth rate (g m^{-2} $°Cd^{-1}$), pod growth rate (g m^{-2} $°Cd^{-1}$), partitioning coefficient (%) and pod yield (g m^{-2}) at final harvest as influenced by daylength (natural daylength, ND, or long days, LD) in three experiments*

	Crop growth rate	Pod growth rate	Partitioning coefficient	Yie
		Experiment 1		
ND	0.84 ± 0.07	0.44 ± 0.01	52.4	482
LD	0.76 ± 0.06	0.24 ± 0.01	31.6	215
			SE ±	
		Experiment 2		
ND	0.74 ± 0.05	0.27 ± 0.02	36.5	334
LD	0.87 ± 0.15	0.12 ± 0.01	13.8	152
			SE ±	15
		Experiment 3		
ND	0.61 ± 0.03	0.11 ± 0.01	18.0	79
NB	0.59 ± 0.04	0.04 ± 0.01	6.8	

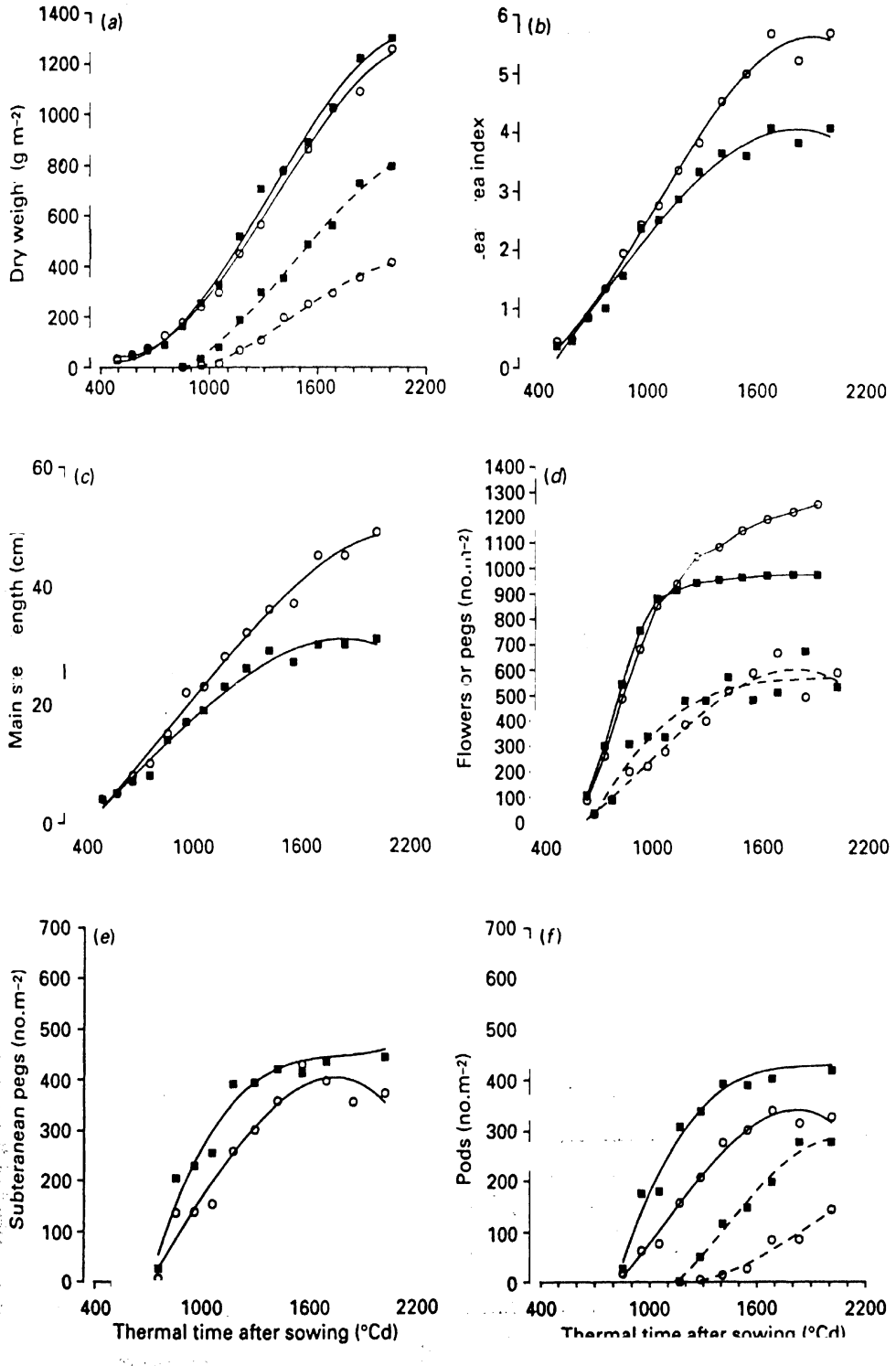

Fig. 1. Changes with thermal time in (a) total biomass (——) and pod mass (----); (b) leaf area index; (c) main stem length; (d) cumulative production of flowers (——) and pegs (----); (e) numbers of pegs penetrating the soil; and (f) numbers of pods (——) and mature pods (----) of groundnut cv. NC Ac 17090 grown in long day (LD, o) and natural daylength (ND, ■) conditions (Experiment 1).

Table 3. *Percentage of recoverable radioactivity in vegetative and reproductive plant parts 24 hours after exposure to $^{14}CO_2$ under natural daylength (ND) and long days (LD) (Experiment 1)*

	Leaf	Stem	Root	Fruit
ND	53	17	6	24
LD	47	26	8	19
SE (±)	1.0	0.9	0.4	2.9

Short days resulted in less leaf area over the reproductive phase (Fig. 1b) in all experiments, although LAI was sufficient (more than 3.5) to intercept 95% of the radiation over this phase of crop growth.

Photoperiod had a large impact on pod yields as a result of changes in PGR (Fig. 1a and Table 2). There was considerable difference in the partitioning between the ND treatments of Experiments 2 and 3, which experienced the same photoperiod but different water supply levels. Although the partitioning coefficient in treatment ND of Experiment 3 was half that observed in Experiment 2 the proportional changes in the partitioning coefficient in response to the LD treatments were almost identical.

In Experiment 1 evaluation of the short-term (24 h) distribution of assimilates using isotope techniques showed that ^{14}C translocation to roots was not decreased by long days (Table 3), and supported the long-term partitioning of assimilates observed by growth analysis (Table 2). The effect of daylength on the distribution of assimilates between pods and stems was reflected in the increase in main axis length in treatment LD (Fig. 1c). The stem lengths were very similar over the first half of growth, but significant differences developed after 1200°C d.

Plants started flowering after 535°C d in all experiments. The impact of photoperiod on flowering was confined to late flower production (Fig. 1d). Final peg numbers initiated increased with thermal time between 660°C d and about 1250°C d (Fig. 1d). Although differences were not significant at any one sampling date, plants in treatment ND consistently had more pegs than those in treatments LD between 850 and 1500°C d. The rate of peg penetration into the soil (Fig. 1e) was also influenced by photoperiod, partly because of its effects on total peg production.

Pod production (Table 4) commenced about 860°C d after sowing in all the experiments, but the rate of production over the linear phase, and final pod number, were strongly affected by photoperiod (Fig. 1f) in each experiment. Maturation of the pods was strongly influenced by photoperiod in Experiments 1 and 2 (Fig. 1f). Mature pod numbers were very variable across time in Experiment 3, so only the data of Experiments 1 and 2 were analysed for the effects of DL on the time taken for pods to mature. Although the first pods were initiated at the same time (850°C d) in both treatments, mature pods were observed earlier, and their numbers increased faster, in treatment ND than in treatment LD (Fig. 1f). The thermal time required for single fruits to mature

Table 4. *Rate of pod production (m^{-2} °Cd^{-1}) and total pod number at final harvest under natural daylength (ND) and long days (LD) ($r^2 > 0.80$)*

	Pod production rate	Final pod number
	Experiment 1	
ND	0.63 ± 0.09	418
LD	0.47 ± 0.03	327
		SE ± 15.3
	Experiment 2	
ND	0.52 ± 0.02	560
LD	0.42 ± 0.40	386
		SE ± 33.4
	Experiment 3	
ND	0.52 ± 0.14	315
NB	0.36 ± 0.02	165
		SE ± 4.8

Table 5. *Kernel growth rate (g m^{-2} °Cd^{-1}), single kernel growth rate (mg $seed^{-1}$ °Cd^{-1}) and kernel yield (g m^{-2} at 142 DAS) under natural daylength (ND) and long days (LD)*

	Kernel growth rate	Single kernel growth rate	Kernel yield
	Experiment 1 ($r^2 > 0.88$ N = 8)		
ND	0.37 ± 0.01	0.40 ± 0.02	346.1
LD	0.16 ± 0.01	0.30 ± 0.03	147.7
	Experiment 2 ($r^2 > 0.91$ N = 8)		
ND	0.20 ± 0.023	0.16 ± 0.033	212.4
LD	0.09 ± 0.014	0.19 ± 0.021	80.9

in Experiments 1 and 2 increased with mean DL (Fig. 2a), the response to extra daylength being similar in each experiment although there were considerable differences in the intercept term.

Kernel mass also showed considerable variation across sampling dates in Experiment 3, so only the results of Experiments 1 and 2 are presented in Table 5. Kernel growth rate was reduced by 57% in treatment LD and resulted in a similar reduction in kernel yield, closely following the effects of photoperiod on PGR. The effects of photoperiod on single kernel growth rate were, however, inconsistent between experiments.

DISCUSSION

These experiments describe the phenological basis for photoperiod effects in groundnut. The initiation of a pod is the outcome of a number of sequentially dependent steps (Smith, 1950). First, a flower is initiated, expands and is

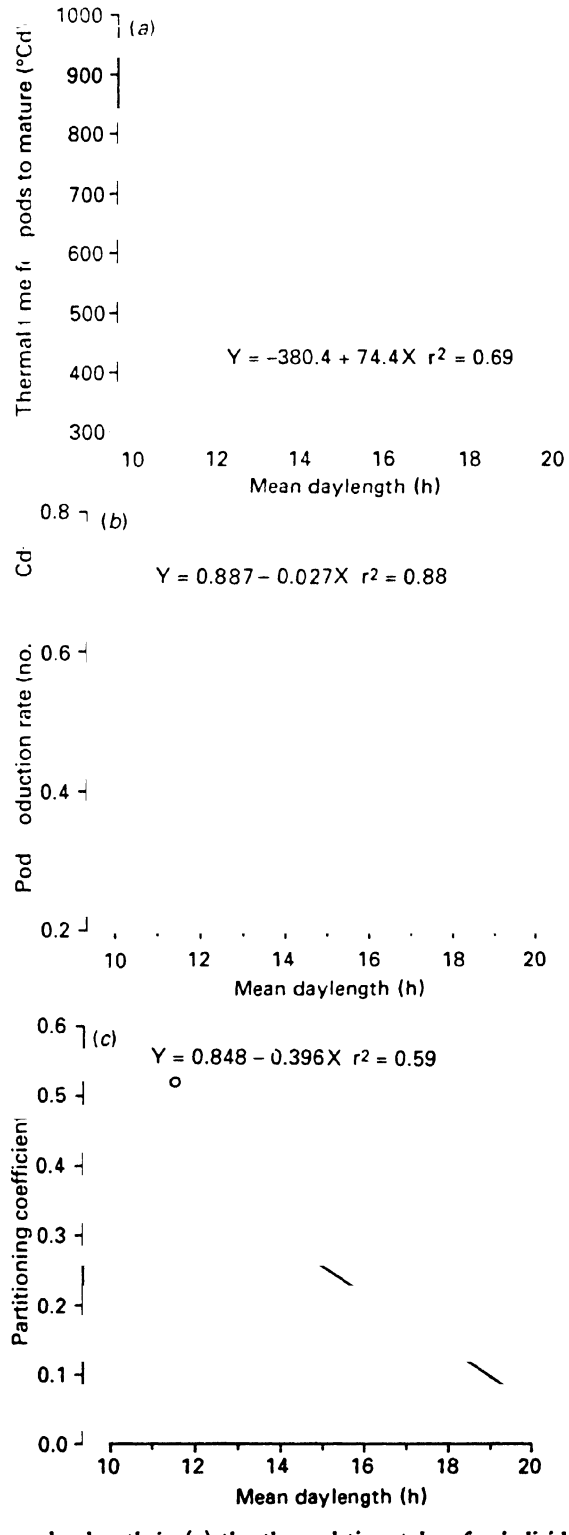

Fig. 2. Changes with mean day length in (a) the thermal time taken for individual pods to mat the pod initiation rate; and (c) the partitioning coefficient for groundnut cv. NC Ac 17090 (Expe 1, ■, 2, o, and 3, *).

fertilized; the rate of flower appearance was not influenced by photoperiod. The peg then starts growing towards the soil, but pod development will not occur until the peg has grown some distance (about 5 cm), into the soil. Although total peg numbers were similar in both photoperiod treatments, natural daylehgth (ND) resulted in more pegs and subterranean pegs over the first half of reproductive growth than long days (LD) because of the initially higher rates of production. The development of the pods from subterranean pegs was also influenced by photoperiod, being slower in long days than in natural daylength. Thus, the smaller final numbers of pods in long days was due to the photoperiod effect on all developmental processes after flowering, which all occurred at a slower rate in long photoperiods, the effects being cumulative. The rate of pod production plotted against the average daylength of all the experiments showed that the rate of this process was strongly related to daylength (Fig. 2b), and that the response of pod production to photoperiod was linear.

The possibility of the shoot meristems being a more powerful 'sink' in the long days (and so limiting peg development by competing for assimilates) seems an unlikely explanation of the photoperiod effect because the greater stem length and LAI in long days developed only after reproductive growth had started, as the differences in fruit numbers were being established. Also the roots had an increased $^{14}CO_2$ content in the long day conditions, suggesting that there was no decrease in the movement of assimilate past the reproductive primordia that could be attributed to greater competition by the shoot meristems. Thus, the failure of NC Ac 17090 to partition assimilates into fruit in long days was most probably caused by the failure to produce adequate pod numbers.

In these experiments long days did not consistently increase the CGR, suggesting that the earlier observation (Witzenberger *et al.*, 1988) of such an effect was the result of variations in energy interception associated with canopy development rather than the effect of decreased partitioning to roots (that were not included in the estimation of CGR). The ^{14}C tracer distribution in Experiment 1, and measurement of total root mass (Flohr, 1989), support this hypothesis.

Partitioning was influenced by daylength in much the same way as observed for this variety by Witzenberger *et al.* (1988). However, there was a wide range of partitioning co-efficients observed across the experiments. These variations were also linearly related to daylength (Fig. 2c).

The effect of photoperiod on the time that pods take to mature (Fig. 2a) explains the changes in shelling percentage and seed size observed by Witzenberger *et al.* (1985) in response to long day conditions, and may be a factor in the differential growth duration of pods set at different stages of the pod setting process (Williams, 1979). This effect clearly is of major importance to the adaptation of the crop to different photoperiod regimes. The response is consistent with the ecological requirements of a tropical legume, in that maturity

would be hastened as the crop approached the normally dry winter months of the semi-arid tropics.

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